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EFFECTS OF CLIMATIC VARIABILITY ON HERBACEOUS PHENOLOGY AND OBSERVED SPECIES RICHNESS IN TEMPERATE MONTANE HABITATS, LAKE TAHOE BASIN, NEVADA

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ABSTRACT

Surveys of herbaceous flora found in flower in the eastern central Sierra Nevada (Nevada) demonstrated the influence of climate variability on herbaceous phenology and observed species richness. Mid-summer surveys conducted in two climatically different years showed differences in number of flowering species (greater in the wetter year) and their characteristic phenological class (more early- vs. late-flowering species in the wetter year). Between year variation in phenology and species richness appeared to be keyed to snowpack duration, spring and summer moisture availability, and early growing season temperatures. Responses in mesic habitats were greater than in xeric sites. Phenological responses to climate variability can be interpreted in terms of displacement, compression, and amplification of the phenological cycle. Comparison of the two surveys suggests that both displacement and amplification generated observed differences. In the wetter year, late snowpack and lower spring temperatures delayed flowering times and greater spring and early summer moisture resulted in greater observed species richness. Sensitivity of herbaceous species in these montane habitats to year-to-year differences in climate highlights the importance of considering effects of climate variability on phenology and population dynamics in short-duration plant biodiversity surveys and long-term monitoring programs.

INTRODUCTION

Climate variability strongly affects population, community, and ecosystem processes in herbaceous systems (e.g., Tilman and El Haddi 1992; Walker et al. 1994). Stand phenological responses to interannual variability in thermal, moisture, and light regimes can be dramatic, reflecting seasonal dynamics of species reproductive cycles, community composition, and plant production. Understanding the herbaceous response to interannual climate variability and identification of key surface climate factors controlling this response can reveal the sensitivity of the herbaceous component of plant communities to short-term climate variation and directional climate change. This understanding can, in addition, aid in evaluating the representativeness of rapid biodiversity assessments and design of long-term monitoring studies.

In temperate regions, soil and air temperature, moisture availability, photoperiod, and, in areas receiving snow, snowpack duration are common controls over growth initiation and timing of subsequent phenophases (Holway and Ward 1963, 1965; Lieth 1974; Dickinson and Dodd 1976; Pitt and Heady 1978; Schemske et al. 1978; Bertiller et al. 1990). In mountain environments of western North America, one of the strongest interannual climatic signals is that of winter snowpack. The strength of this signal is derived from the effect of quasi-periodic interannual variations in tropical and mid-latitude Pacific sea surface temperatures on the strength and tracks of winter storms, such as associated with El Niño and the North Pacific Oscillation (Ropelewski and Halpert 1986; Sheaffer and Reiter 1985).

The objective of this study was to understand the phenological response of the herbaceous component of several montane communities in the eastern central Sierra Nevada (Nevada) to interannual snowpack variation and associated variation in temperature. The approach was to analyze changes between two plant surveys, one conducted in a low snowpack year and the other in a high snowpack year, in terms of (1) differences in the number of species found in flower and predominant phenological class of these species and (2) whether these responses varied by habitat.

METHODS

Study area. The plant surveys were conducted in the Sierra Nevada montane forest belt on the eastern side of the Lake Tahoe Basin, Nevada. The study area covered four watersheds: Skunk Harbor, Slaughterhouse Canyon, Marlette Creek, and Spooner Lake (Fig. 1). These sites were chosen to capture a wide variety of vegetation types characteristic of this montane region. The predominant type is East-slope Jeffrey Pine Forest as described by Rundel et al. (1980), with dominance shared by *Pinus jeffreyi, P. ponderosa, Abies concolor,* and *Calocedrus decurrens.* The forest is generally open, reflecting a relatively xeric environment.

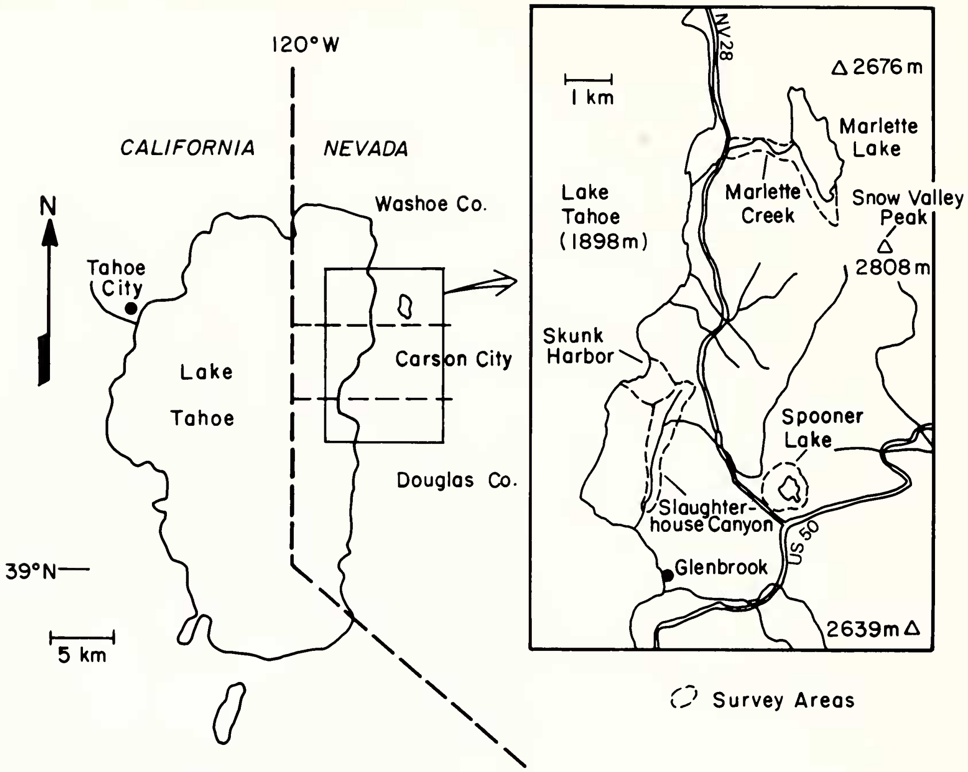

FIG. 1. Location of the survey area in the Lake Tahoe Basin, California-Nevada. The four survey sites are indicated by enclosed short-dashed lines on the detailed map.

Each watershed also contains varying amounts of other vegetation types. Skunk Harbor (elevation range 1900–2000 m) includes narrow riparian communities and montane chaparral with *Arctostaphylos patula* and *Chrysolepis sempervirens* (see Smith 1973; Ornduff 1974). The Slaughterhouse Canyon site (1920–1990 m) has extensive montane meadows and adjacent stands of *Pinus contorta* ssp. *murrayana.* Vegetation of the Marlette Creek watershed (1970–2440 m) is predominantly Jeffrey Pine Forest with a transition at higher elevations to Red Fir (*Abies magnifica*) Forest (Rundel et al. 1980). The Spooner site (2120–2150 m) includes a large meadow surrounding Spooner Lake, that grades from wet meadow dominated by *Carex* spp. to dry meadow (Rundel et al. 1980; Smith 1973), and an adjacent sagebrush scrubland (Smith 1973) dominated by *Artemisia tridentata.*

Surveys. Gordon and Dossman (1968) undertook a presence-absence survey of non-graminoid herbaceous species across the study area in 1968. In the following year, I repeated their survey to evaluate how the findings of such efforts might vary between two climatically-different years (Kittel 1969). Both 1968 and 1969 surveys spanned the first week of July. One observer from the first survey (J. Gordon) assisted in the second. This facilitated consistency in both diversity and areal coverage of vegetation types sampled within each watershed. The surveys recorded presence or absence of non-graminoid herbaceous species that were in flower during repeated walk-throughs in each area. As an indicator of species habitat, the surveys recorded vegetation type (e.g., wet meadow, Jeffrey Pine Forest, montane chaparral) for each species recorded. The original taxonomic authority was Munz and Keck (1973); taxonomy presented in this paper was updated to Hickman (1993).

Differences between years in total area sampled across watersheds and by vegetation type could not be quantified, potentially limiting the significance of results. However, coverage of the study area was extensive, widely sampling each watershed and vegetation type in both years. In general, sampling of each vegetation type was continued until no or very few additional species were found on visits to different parts of a watershed. As a result, between-year differences in the total area surveyed within a watershed or by vegetation type likely had only small systematic effects on the number and phenological class of species found.

Climate data. As representative measures of climate for the region, I used monthly and daily temperature and precipitation data for Glenbrook, Nevada (elevation 1915 m; Fig. 1) and precipitation and snow depth data from Spooners Station (2142

m) near Spooner Lake (U.S. Environmental Data Service 1967, 1968, 1969a, b, 1970, 1973; U.S. Weather Bureau 1965). I calculated growing degree days from mean daily temperatures with a base temperature of 0°C.

Analyses. I classified the species into early- and late-flowering taxa based on flowering times given by Munz and Keck (1973). While the given flowering times span those observed over the elevational extent of a species, they indicate a species' tendency toward early- vs. late-flowering. Because the surveys were made in early July, I defined early-flowering species as those with flowering periods centered on June or earlier and late-flowering species as those with flowering periods centered on July or later. I included species with June–July flowering periods in the early-flowering class. I omitted from the classification 21 species with broadly specified flowering times overlapping this division.

I compared the 1968 and 1969 frequency distributions of early- vs. late-flowering classes for in-flower species that were unique to a year for each of the sites. I used a chi-square (χ^2) test for independence (Conover 1980; SPSS and Norušis 1986) to test the null hypothesis that the distribution of unique species between early- and late-flowering categories was the same for the two years.

In addition to the site-by-site analysis, I employed three analyses on data combined across sites. First, in a combined-flora analysis, I determined whether a species was unique to a year based on 1968 and 1969 species lists combined across all sites. I evaluated flowering class distributions of these unique species in a χ^2 analysis as in the site-by-site analysis. This test was more conservative than the site-by-site analysis because species unique to a year at one site were omitted if they were present for the other year at other sites.

Second, in a pooled-distribution analysis, I summed the distributions of flowering time classes across all sites and evaluated the pooled distribution with a χ^2 test. This was a more powerful test than the combined-flora analysis because the response patterns of each site were represented in the analysis.

In a third cross-site analysis, I evaluated whether habitat influenced phenological responses to climate variability across the study area. I stratified unique species into two habitat classes based on broadly-defined "mesic" and "xeric" groupings of vegetation types. This stratification reflects a simple but clear distinction in habitats across the study area. I analyzed pooled flowering class distributions for each habitat class with a χ^2 test. Habitat classes based on vegetation type were as follows: mesic habitats included forest-meadow edge, wet and dry meadow, and riparian areas, while xeric habitats included conifer forest, chaparral, and sagebrush scrubland. Although vegetation type is only one descriptor of a species' habitat, vegetation type tended to co-vary across the landscape with other site characteristics (slope, aspect, drainage, and soil). Mesic vegetation types tended to be on less well drained sites with more developed finer soils. Xeric types were found on steep slopes with poorly developed coarse soils (e.g., decomposed granite). A benefit of this analysis is that stratification by habitat class helped to remove possible systematic differences between years in areal coverage of vegetation types.

RESULTS

Mean climate. The long-term mean maximum temperature for the warmest month (July) at Glenbrook was 28.2°C and mean minimum for the coldest month (January) was −5.0°C (Fig. 2a). Long-term mean annual precipitation for Glenbrook was 487 mm. The seasonal cycle of precipitation has a winter maximum characteristic of Mediterranean climates (Fig. 2a). Winter precipitation is generated by mid-latitude cyclonic storms from the Pacific and generally falls as snow at this elevation. There is a second, smaller precipitation peak in late spring (around May) that is evident in records for individual years (Fig. 2b). This peak is not distinguishable in the mean pattern (Fig. 2a) because of variability in its timing. This secondary maximum is common at higher elevations of the central and southern Sierra Nevada and is largely due to convective precipitation associated with greater surface heating and conditionally unstable air associated with late spring weak cyclones from the Pacific (Pyke 1972). Summer climate is dominated by dry subsiding air from the eastern Pacific subtropical high pressure center, with only occasional rainfall from convective storms.

Climate variability. There was high variability in monthly precipitation and temperatures among years 1967, 1968, and 1969 at Glenbrook (Fig. 2b). For the 1967–1968 water year (July–June), that is, for the 12 months prior to the 1968 survey, precipitation totalled 443 mm, or 91% of the long-term mean. In contrast, the 1968–1969 water year precipitation was 771 mm, or 158% of the mean. This interannual difference was also reflected in Spooners Station precipitation and snow depth records (Fig. 3). Snowpack was greater in 1969 than in 1968 (e.g., 152 cm on 15 February 1968 vs. 221 cm on the same date in 1969; Fig. 3a). Snow cover lasted at Spooners through early April in 1969 versus through the end of February in 1968 (Fig. 3a).

Timing of the spring precipitation maximum at Glenbrook was one month later in 1969 than in 1968 (June vs. May, Fig. 2b). The month shift in 1969 spring precipitation was not an artifact of dividing the record into months when constructing means: daily precipitation data showed that the spring minimum and maximum in each year were well centered in the indicated months. Timing of

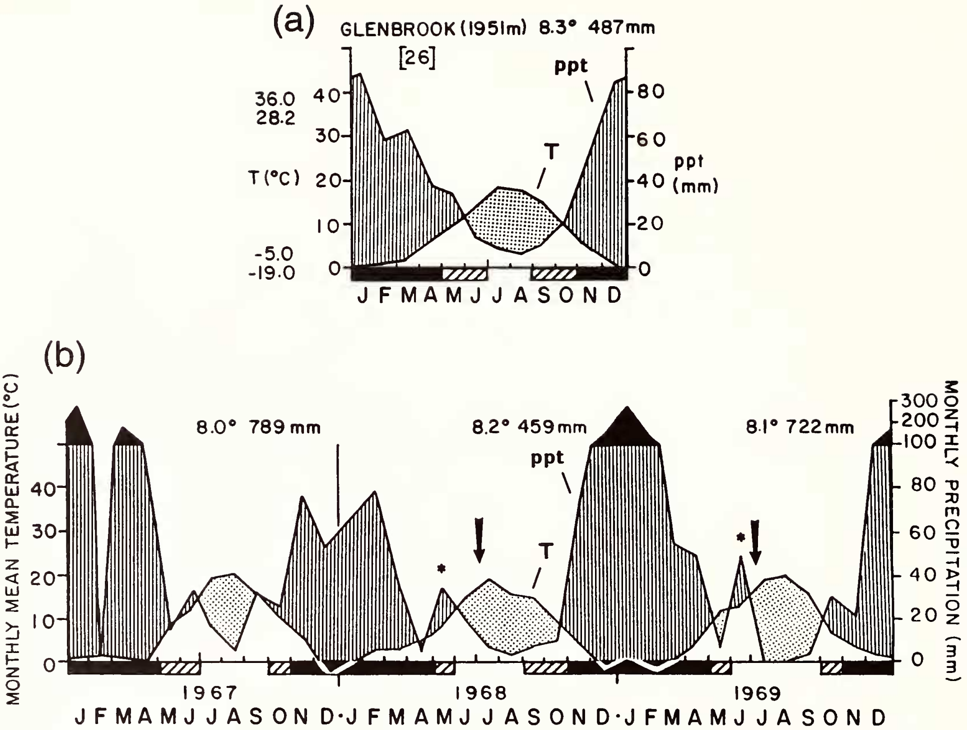

FIG. 2. Walter (1985) climate diagrams for Glenbrook, Nevada. (a) Long-term (1945–1970) mean temperature (T; left axis) and monthly precipitation (ppt; right axis). (b) Monthly mean temperature and monthly precipitation for 1967, 1968, and 1969. Arrows mark survey periods (first week in July) and asterisks (*) indicate the spring precipitation maxima preceding each survey. Vertically-hatched areas indicate periods of water surplus and stippled areas those of water deficit as defined by Walter (1985). Bars under the x-axis show months with mean daily minimum temperature < 0°C (solid bar) and months with absolute monthly minimum < 0°C but mean daily minimum > 0°C (diagonally-hatched bar). Solid area under the precipitation curve in (b) denotes a scale change in the precipitation axis. The two values above each year's plot in (a) and (b) are the mean annual temperature (°C) and annual precipitation (mm/y). In (a), the value given in square brackets is the number of years in the record, and values to the left of the plot are, from top to bottom, highest temperature in the record, mean daily maximum of the warmest month, mean daily minimum of the coldest month, and lowest temperature in the record.

the spring maximum is critical because it generally marks the end of the precipitation season.

Between year variability in early season temperatures was reflected in growing degree-days. 1968 had more growing degree-days from January through June than did 1969 (1136 vs. 1019°C-days). Average temperature in June, the month just prior to the surveys, was greater in 1968 than in 1969 (15° vs. 13.3°C). In summary, the water year prior to the 1968 survey was warmer, drier, and snow-free earlier than that preceding the 1969 survey.

Survey comparison. The surveys identified 105 species in 30 families (Table 1). The survey in 1969 found significantly more species (88 species) than that in 1968 (75 species; $P < 0.0015$, df = 3, 1-tailed paired Student's t-test). The number of both early- and late-flowering species also increased significantly from 1968 to 1969 ($P < 0.0001$ and 0.05, respectively). Of the total number of species found combined from both years, a higher portion was unique to the 1969 survey than to the 1968 survey (29% vs. 16%). At individual sites, species unique to the 1969 survey accounted for up to more than half of the species found (Table 1).

Early-flowering species dominated both surveys, but more so in 1969 than in 1968. The ratio of early- to late-flowering species was 1.15 in 1968 and 1.56 in 1969. For species unique to each survey, the frequency distribution of flowering times differed between years (Fig. 4a). At each site, unique species were predominantly late-flowering in 1968 and early-flowering in 1969. The strength of this relationship varied between sites, ranging from statistically significant at the 0.05 level (Spooner Lake) to not significant (Marlette Creek) (Fig. 4a). The shift in dominance across sites from late to early species from 1968 to 1969 was strongly supported by the combined-flora analysis ($\chi^2 = 4.3$, $P < 0.05$, df = 1; Table 2) and the pooled-distribution analysis ($\chi^2 = 10.6$, $P < 0.0015$, df = 1).

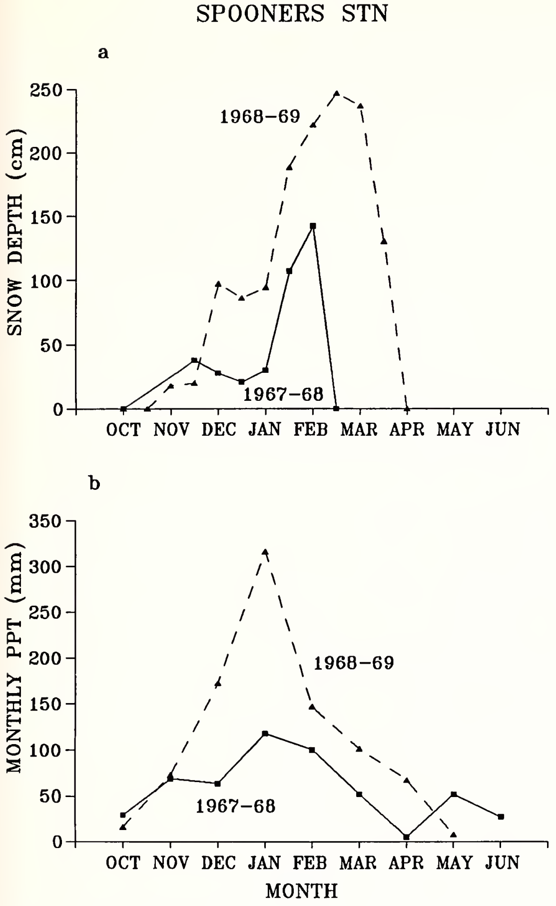

FIG. 3. (a) Biweekly snow depth and (b) monthly precipitation at Spooners Station for 1967–1968 and 1968–1969 winters. X-axis ticks in (a) mark the 15th of each month. Precipitation data for June 1969 were not available.

Weak differences at the site level may have arisen from the variety of habitats within sites and because different habitats responded differently to climate variability. Consequently, phenological shifts may have been stronger than observed, but were blurred because sampling at each site ranged across habitats. In the analysis by species' habitat pooled across sites, both habitat classes showed a significant difference in flowering class frequencies between years (Fig. 4b). The response was stronger for mesic habitats ($\chi^2 = 11.4$, df = 1, $P < 0.001$) than for more xeric habitats ($\chi^2 = 6.0$, df = 1, $P < 0.015$). In addition, both habitats showed an increase from 1968 to 1969 in the number of unique species found, with xeric habitats having a larger increase (from 12 to 50 species pooled across sites) than mesic habitats (9 to 26).

The effect of habitat on flowering class response was also reflected at the site level. Slaughterhouse Canyon and Spooner Lake sites, dominated by wetter habitats (meadow and riparian), had greater flowering class shifts, as shown by the magnitude of corresponding χ^2's (4.5 and 3.7, respectively; Fig. 4a), than Skunk Harbor ($\chi^2 = 2.6$) and Marlette Creek ($\chi^2 = 0.5$), dominated by conifer forest and montane chaparral.

TABLE 1. NUMBER OF SPECIES, TOTAL AND UNIQUE, FOR THE 1968 AND 1969 SURVEYS AND FOR BOTH YEARS COMBINED. The percent of unique species relative to the combined total is given in parentheses.

Site	Combined total	1968 Survey		1969 Survey	
		Total	Unique to year	Total	Unique to year
Skunk Harbor	49	25	6 (12%)	43	24 (49%)
Slaughterhouse Canyon	71	41	7 (13%)	64	30 (42%)
Spooner Lake	75	45	14 (19%)	61	30 (40%)
Marlette Creek	57	26	5 (9%)	52	31 (54%)
All sites	105	75	17 (16%)	88	30 (29%)

DISCUSSION

Modes of phenological response to climate variability. Phenological response of herbaceous species to variation in climate can be in terms of altered phenophase timing (displacement), duration (phase compression or extension), and amplitude (phase amplitude modulation) (Fig. 5). In displacement, timing of phenophases is delayed or advanced, so that the flowering season occurs later or earlier in the year (Fig. 5a). On the other hand, if the growing season is shortened or lengthened, the duration of phenophases may be compressed or extended, respectively (Fig. 5b). With compression, for example, the phenological cycle is completed more rapidly so that the flowering period starts later and ends earlier. In amplitude modulation, the timing and length of the phenological cycle are not altered, but the number of individuals per species and number of species observed in a given phenophase is amplified or reduced (Fig. 5c). In amplification, favorable conditions enhance plant growth, flower production, or other physiological and population factors that increase the number of species observed in flower at a given time.

Comparison of the 1968 and 1969 surveys suggests that both displacement and amplitude modulation were important in generating observed differences. In 1969, prolonged snowpack and later spring precipitation delayed plant phenologies so that substantially more early-flowering than late-flowering species were in flower during July. In 1968, below normal winter and spring precipitation and more growing degree-days advanced plant phenologies and increased the number of late-flowering species in blossom in July. Other studies have observed phenological displacement in winter-snow environments, where delayed snowpack melt delayed initiation of growth and flowering in early

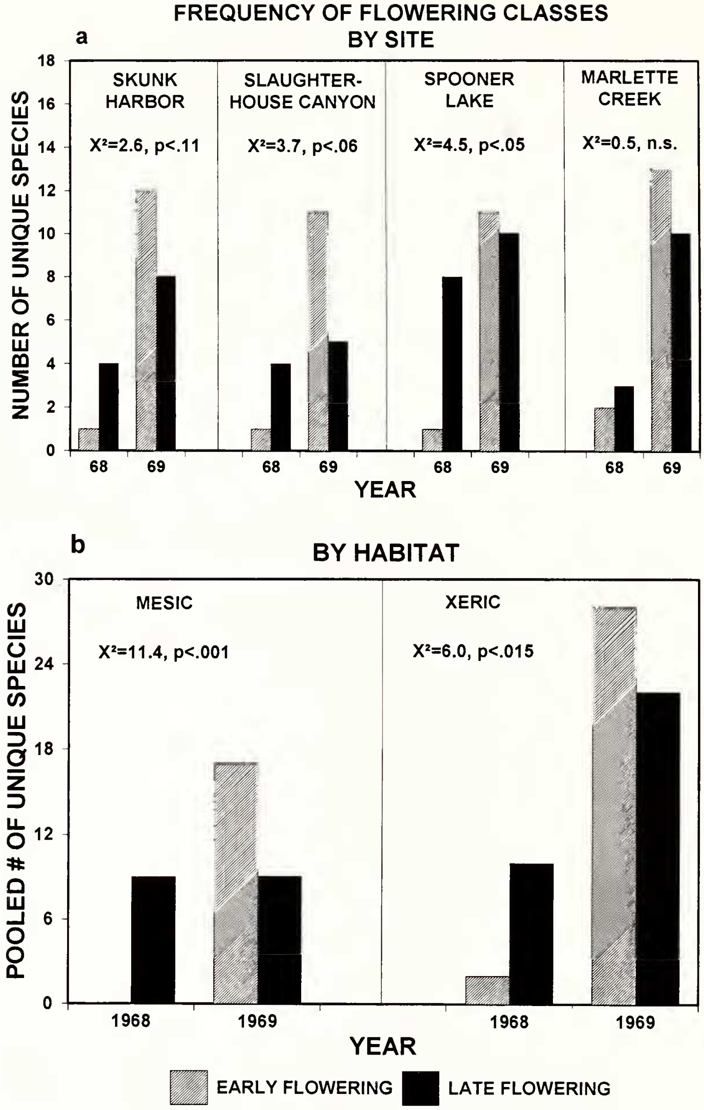

FIG. 4. Frequency distribution of early- and late-flowering classes for species unique to either 1968 or 1969 surveys (a) by site and (b) by mesic vs. xeric habitats pooled across sites. Chi-square values (χ^2) and significance levels (p) are given (df = 1). ns = not significant. In (b), the y-axis is number of unique species pooled (summed) across sites.

season species (Holway and Ward 1965; Owen 1976).

The greater number of both early- and late-flowering species found in flower in 1969 may have resulted from phenophase amplification. Better spring and early summer moisture conditions in that year possibly resulted in greater population sizes or greater flower production, increasing the likelihood of less common species being included in the 1969 survey. Jackson and Bliss (1984) also found phenophase amplification in a subalpine meadow where greater mid-season precipitation increased recruitment, growth, flowering, and seed set.

Phenophase duration responses may have also occurred but cannot be demonstrated by the 1968–1969 comparison because of the short, single sampling period used by the surveys. This response has been observed in other winter-snow environments including alpine communities (Holway and Ward 1965; Billings and Bliss 1959). In the extremes, a severely shortened growing season can lead to truncation of phenologies for late season species (Holway and Ward 1963), while an unusually prolonged growing season can lead to early season species completing all or part of a second cycle in a year (Holway and Ward 1965; Dickinson and Dodd 1976).

While analysis of phenological responses in terms of these three modes is a useful approach for understanding observed variation as a function of

TABLE 2. SPECIES UNIQUE TO EITHER 1968 OR 1969 SURVEYS BY EARLY VS. LATE-FLOWERING CLASS ACROSS ALL SITES. Species with broadly defined flowering periods were omitted. Nomenclature follows Hickman (1993). Growth habit (from Hickman 1993) is given: A = annual, B = biennial, P = perennial, and P/ = perennial, dies after flowering once; introduced (I) or possibly introduced (I?) species are also indicated.

Collection year	Early flowering		Late flowering	
	Species	Habit	Species	Habit
1968 only	*Brassica rapa* L.	A (I)	*Angelica breweri* A. Gray	P
	Lepidium virginicum L. var. *pubescens* (E. Greene) Thell.	A	*Antennaria rosea* E. Greene	P
	Tragopogon porrifolius L.	B (I)	*Ipomopsis aggregata* (Pursh) V. Grant	P/
			Phacelia hastata Lehm. ssp. *compacta* (Brand) Heckard	P
			Polygonum amphibium L. var. *stipulaceum* Coleman	P
			Pterospora andromedea Nutt.	P
			Pyrola minor L.	P
			Stachys ajugoides Benth. var. *rigida* Jepson & Hoover	P
			Trifolium monanthum A. Gray	P
			Veronica cusickii A. Gray	P
1969 only	*Allophyllum gilioides* (Benth.) A.D. Grant & V. Grant ssp. *violaceum* (A.A. Heller) Day	A	*Chamaesyce serpyllifolia* (Pers.) Small	A
	Camissonia contorta (Douglas) Raven	A	*Eriogonum spergulinum* A. Gray	A
	Collinsia parviflora Lindley	A	*Mimulus breweri* (E. Greene) Cov.	A
	Delphinium nuttallianum Walp.	P	*Mimulus mephiticus* E. Greene	A
	Descurainia pinnata (Waller) Britton ssp. *intermedia* (Rydb.) Detl.	A	*Montia chamissoi* (Sprengel) E. Greene	P
	Galium aparine L.	A (I?)	*Penstemon gracilentus* A. Gray	P
	Lewisia nevadensis (A. Gray) Robinson	P	*Saxifraga nidifica* E. Greene var. *nidifica*	P
	Linanthus ciliathus (Benth.) E. Greene	A	*Urtica dioica* L. ssp. *holosericea* (Nutt.) Thorne	P
	Madia minima (A. Gray) Keck	A		
	Mentzelia congesta Torrey & A. Gray	A		
	Paeonia brownii Hook.	P		
	Ranunculus alismifolius Benth.	P		

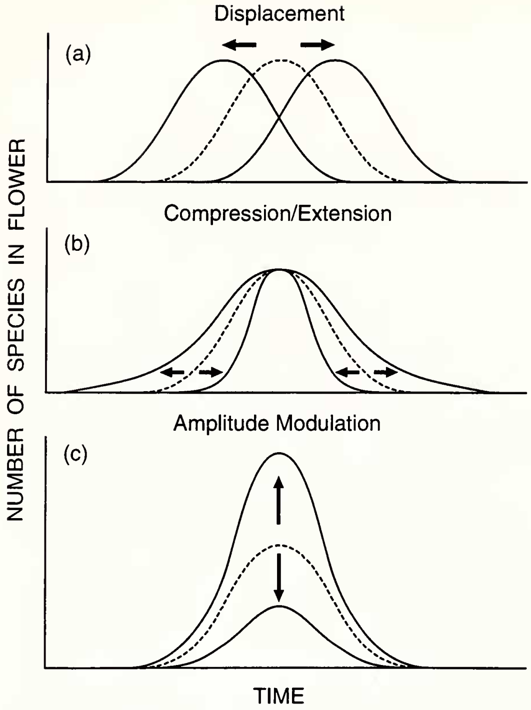

FIG. 5. Idealized phenological response curves. Phenophase (a) displacement, (b) compression and extension, and (c) amplitude modulation are illustrated in terms of number of species in flower during the course of a growing season.

climate, responses may be complex combinations of these modes arising from multiple and interactive effects of temperature and moisture on plant physiology (Walker et al. 1994; Holway and Ward 1965; Jackson and Bliss 1984). Additional complexity arises at the community level because responses are an admixture of species-specific responses moderated by species interactions (Jackson and Bliss 1984). In addition, climate conditions in one year have important carry-over effects to the next through seed set, belowground shoot meristem production in perennial herbs, and, in non-herbaceous taxa, flower primordia production (Scott 1977; Jackson and Bliss 1984; Billings and Mooney 1968; Holway and Ward 1965).

Habitat effects. Habitat type influenced the magnitude of phenological response to climate variability. Phenologies were more delayed in less well drained sites, where higher soil moisture (and cooler soil temperatures) likely persisted longer into the 1969 summer following heavy snowpack and late spring precipitation. In contrast, forest and chaparral areas on slopes with poorly developed soils (primarily decomposed granite) likely dried out earlier, i.e. by mid-summer, than did wetter sites in both years. At these drier sites, greater winter snowpack, late spring rainfall, and associated cooler temperatures in 1969 appear to have resulted in a large increase in the number of flowering species (indicating phase amplification), but a smaller delay in herbaceous phenologies (Fig. 4b).

Key abiotic factors. Differences in survey floras and climate for 1968 and 1969 suggest that herbaceous phenology and observed species richness in the Sierra Nevada montane region are controlled by snowpack amount and duration and early growing season precipitation and temperature. Studies of alpine systems indicate that thawing of soil is the key control over initiation of growth and timing of subsequent phenophases (Billings and Bliss 1959; Billings and Mooney 1968; Holway and Ward 1965; Ram et al. 1988). Increased soil moisture in high snowfall years is an additional control over phenology in these systems, increasing production and delaying senescence on drier sites (Holway and Ward 1965).

Interaction among abiotic factors is critical to understanding seasonal dynamics of montane herbaceous communities because direct effects of changes in a factor may be either amplified or countered by indirect effects. For example, years with greater winter precipitation tend to have greater and more persistent snowpack, cooler early season temperatures, and greater growing season soil moisture. The negative impact of spring snowpack on growing season length can be more than offset by the positive effect of greater soil moisture (Walker et al. 1994).

Implications for plant biodiversity surveys. Between-year changes observed in this study demonstrate that surveys of herbaceous species need to be designed to account for phenological variability and population and community dynamics driven by climate variability. In rare and endangered plant surveys, effects of climatic variability must be considered to avoid misleading assessments of populations (Gruber et al. 1979; Clark and Dorn 1981; Tilman and Wedin 1991). Weather driven within-season shifts in phenology and population sizes can limit the utility of rapid "snapshot" biodiversity assessments. Likewise, because climate variability can force year-to-year shifts in community composition (Tilman and El Haddi 1992; Pitt and Heady 1978; Borchert et al. 1991), such effects must be considered in long-term studies monitoring the status of plant communities facing threats from local to global environmental change.

These responses emphasize the need to understand the role of climate variability in population and community dynamics that influence the preservation of rare species and maintenance of community diversity. Such environmental variation can play a key role in maintaining species diversity (Jackson and Bliss 1984; Grime 1973) or, in the case of extreme climate events, cause local extinctions of individual species, reducing community richness in the long term (Tilman and El Haddi

1992). The sensitivity of the central Sierra Nevada montane herbaceous species to interannual climate variability suggests that population, community, and ecosystem processes will respond rapidly to climate fluctuations and directional climate change.

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